

The Jiyuan tetrapod fauna of the Upper Permian of China—2. stratigraphy, taxonomical review, and correlation

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Abstract Reexamination of the specimens from the Jiyuan tetrapod fauna, shows that this assemblage is dominated by the pareiasaur *Honania complicidentata* and comprises three chroniosuchian species including *Bystrowiana sinica*, *Jiyuanitectum flatum* gen. et sp. nov., and *Dromotectum largum* sp. nov., one cynodont species and possibly one gorgonopsian. It is roughly correlated to the Ilinskoe Subassemblage of the Sokolki Assemblage of Russia and the *Cistecephalus* Assemblage Zone of South Africa.

Key words Jiyuan, Henan; Upper Permian; Shangshihezi Formation; Chroniosuchia, Pareiasauria, Gorgonopsia, Cynodontia

Young (1979) studied some Late Permian materials from the fossil locality 63024 (Huakedaliang, Dayu Township, Jiyuan City, Henan Province, China) of the Shangshihezi (Upper Shihhotse) Formation and named the fossil assemblage of the locality as the Jiyuan (tetrapod) Fauna (Fig. 1). He listed the following components in this fauna: three labyrinthodont taxa including *Bystrowiana sinica*; two pareiasaurs, *Honania complicidentata* and *Tsiyuania simplicidentata*; the dinocephalian *Taihangshania imperfecta*; the gorgonopsian *Wangwusaurus tayuensis*; and the cynodont *Hwanghocynodon multienspidus*. He correlated this fauna with the Russian Zone III and the South African *Endothiodon* Zone.

Although these specimens are fragmentary, they attracted the attention of later researchers. This fauna was viewed as oldest Permian tetrapod fauna of China before the discovery of Dashankou Fauna (Li and Cheng, 1995; Sun, 1980). Sigogneau-Russell and Sun (1981) pointed out “of the three procynosuchid teeth, one is probably a pareiasaurian, and two others may be cynodonts of a new type”; within the ‘gorgonopsian’ teeth, only two are of doubtful gorgonopsid affinities (not including the type); whereas the tapinocephalid teeth probably represent worn or partially digested pareiasaurian teeth. They suggested that the three synapsid taxa were nomina nuda. Lee (1997) regarded all teeth referred to *Tsiyuania*

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Fig.1 The photo of fossil locality 63024 at Jiyuan, Henan, China
The numbers are the layer number on Fig. 2

simplicidentata and *Honania complicidentata* as pertaining to *Sanchuansaurus*, but the types alone are indeterminate, and both taxa must be declared nomina vana. Lucas (2001) accepted the former taxonomic opinions, but he proposed this fauna and the pareiasaurs from the Sunjiagou Formation were more likely correlated to the *Tapinocephalus* Assemblage Zone of South Africa.

Recently some new material has been collected from the 63024 locality by a crew from Henan Geological Museum, and mostly included individual bones of pareiasaurs. These new pareiasaur materials show many important characters differing from other species of the group and the name *Honania complicidentata* was consequently reestablished (Xu et al., 2014). Based on new discoveries, we prepared some old specimens and examined all specimens to revise their taxonomy and use them for correlation with other faunas.

Institutional abbreviations HGM, Henan Geological Museum, Zhengzhou, Henan, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia.

1 Geological setting

Most known fossils from this locality originate from a thin layer (layer 23), which is dark purple pebbly fine sandstone; although some teeth are also collected from layers 22 and 24, which are dark purple mudstone with calcareous concretion (Fig. 2). These layers were referred to the Sunjiagou Formation in geological mapping when the cherts were used as a marker of the Shangshihezi Formation, but in recent years the base of the Sunjiagou Formation was moved to the red beds and these layers should be referred to the Shangshihezi Formation (Xiao, 1985; Wu, 1997).

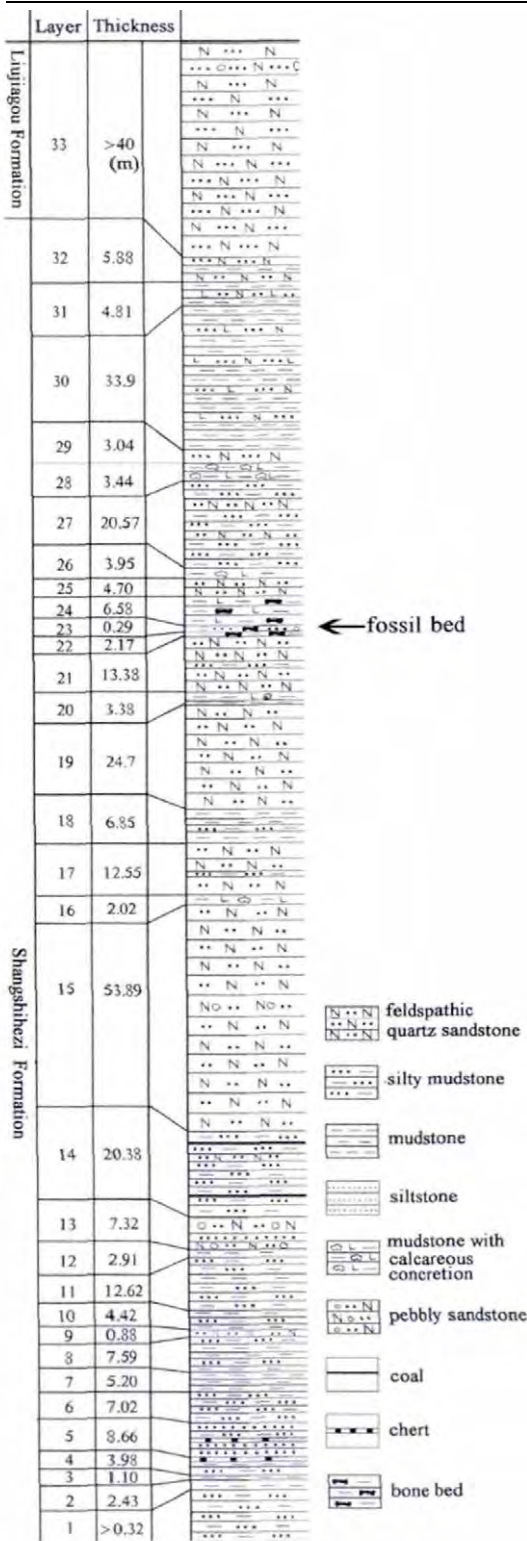


Fig. 2 Lithological column of the 63024 locality

All fossil bones are disarticulated and many are incomplete. Only some parts of the cranial elements have been collected. Disarticulation suggests that the elements underwent transit before burial.

2 Systematic paleontology

Chroniosuchia Tatarinov, 1972

Bystrowianidae Vjuschkov, 1957

***Bystrowiana sinica* Young, 1979**

Holotype IVPP V 4014.1, a small armor scute.

Referred specimen IVPP V 4014.3-4, two armor scutes; HGM 41HIII0445, a vertebra lacking neural spine.

Revised diagnosis Differentiated from *B. permira* by more concaved scute, more ridges on the dorsal facets of the anterior wing.

Description The holotype is incomplete, losing the posterior articulating area and right anterior wing (Fig. 3.2). It is small, the complete size is around 3/5 the size of PIN 1100/9 (Fig. 3.1). This scute is slightly narrower and more concave than PIN 1100/9. The dorsal facet of the anterior wing has three smooth longitudinal ridges and grooves and some rugose ridges laterally. Two ridges extend posteriorly and continue as longitudinal ridges of the sculpture. The sculpture pattern is similar to PIN 1100/9, with longitudinal and transverse orientation of pit walls. The specimens IVPP V 4014.3-4 are poorly preserved but similar to the holotype.

A dorsal vertebra, HGM 41HIII0445, is corresponding to the size of the holotype (Fig. 4.2). Its shape is almost identical to the vertebral shape of *B. permira* (Fig. 4.1). The anterior and posterior margins of the

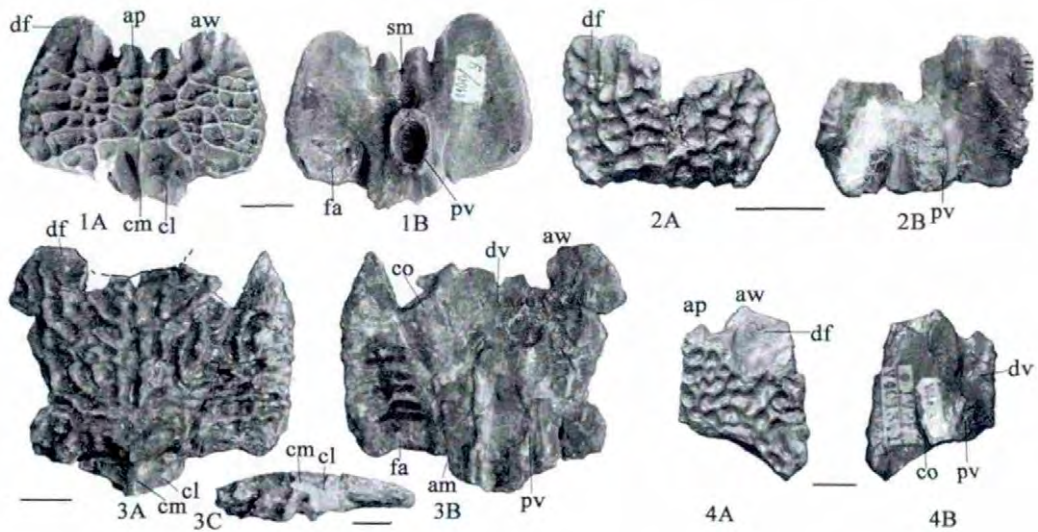


Fig. 3 Armor scutes in dorsal (A), ventral (B) and posterior (C) views

1. *Bystrowiana permira*, PIN 1100/9; 2. holotype of *B. sinica*, IVPP V 4014.1; 3. holotype of *Jiyuanitectum flatum* gen. et sp. nov., HGM 41HIII0444; 4. holotype of *Dromotectum largum* sp. nov., IVPP V 4013.1
scale bars equal 1 cm

Abbreviations: am. area marginalis; ap. accessory process; aw. anterior wing; cl. lateral crista; cm. medial crista; co. oblique crista; df. dorsal facet; dv. ventral depression; fa. facies alaris; pv. ventral process; sm. medial sulcus

pleurocentrum and the prezygapophyses are damaged, and the transverse processes and the neural spine are broken. The centrum is not perforated by the notochord. The neural arch is fused to the deeply amphicoelous pleurocentrum. The zygapophyses are widely spaced. The zygapophyseal facets slope medially at an angle of 20° to the horizontal plane in anterior view. Two pairs of paraneural canals at the base of the zygapophyses are well developed, but the posterior opening of the dorsal pair seems larger and more laterally positioned. The neural canal is compressed dorsoventrally. The transverse process lies above the pleurocentrum, with anteroposteriorly extended base.

Discussion The scute and vertebra can be referred to Bystrowianidae based on the narrow scute bearing broadly separated anterior facets overlapped by preceding plate, paired deep paraneural canals on anterior and posterior surfaces of neural arch, without continuous notochordal perforation (Novikov et al., 2000). Bystrowianidae is showed as a natural group including five genera in the recent study of Buchwitz et al. (2012). Within Bystrowianidae, the specimens are more similar to *Bystrowiana permira* than other taxa in the sculpture pattern, plate broader than long, and zygapophyseal facets slope medially at an angle of 20° to the horizontal plane in anterior view (Novikov and Shishkin, 2000; Novikov et al., 2000; Witzmann et al., 2008). It differentiates from the Russian species by more concaved scute, and more ridges on the dorsal facets of the anterior wing. So the original taxonomical designation is applied.

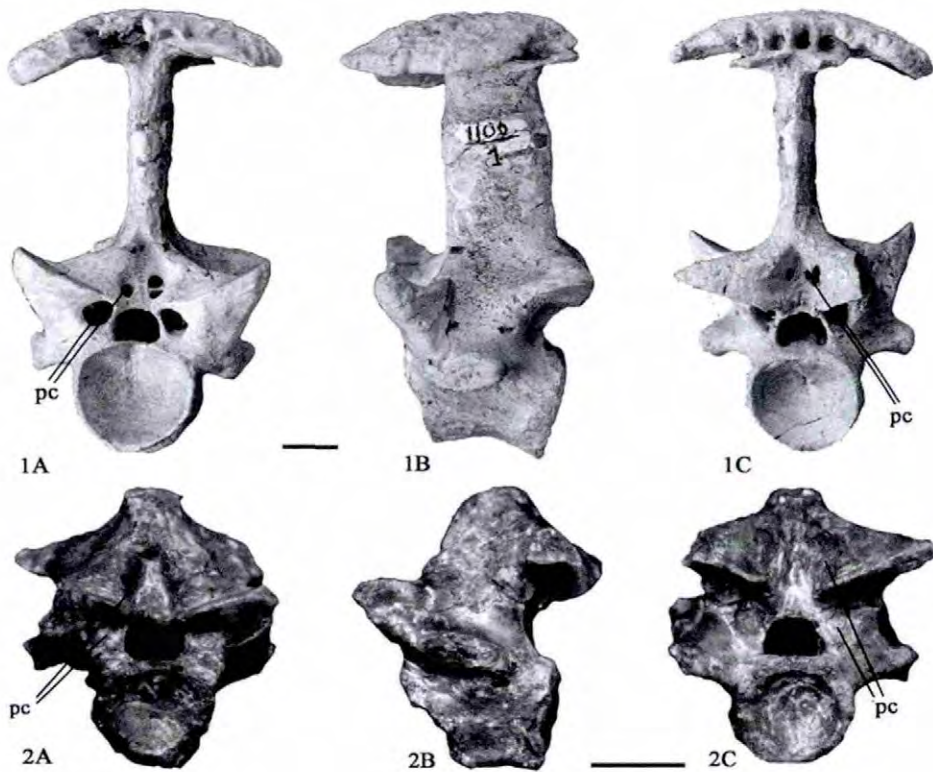


Fig. 4 The vertebrae of *Bystrowiana* in anterior (A), lateral (B), and posterior (C) views
 1. *B. permira*, PIN 1100/1; 2. *B. sinica*, HGM 41HIII0445; scale bars equal 1 cm
 Abbreviation: pc. paraneural canal

Jiyuanitectum flatum gen. et sp. nov.

Etymology ‘Jiyuan’, the city; ‘tectum’, Latin for roof; ‘flatum’, Latin for flat.

Holotype HGM 41HIII0444, a large armor scute; locality 63024, Jiyuan, Henan, China; Shangshihezi Formation.

Diagnosis Large bystrowianid with autapomorphies: lateral margin convex while middle portion nearly straight, shallow median axial groove, and axial crest lying slightly dorsal to lateral crests on posterior articular plate; shares derived characters with *Synesuchus* and *Bystrowiella*: presence of smooth oblique crests, the sculpture surface formed by oblique and transversely sharp ridges.

Description A large scute (HGM 41HIII444) is nearly flat and its anterior, left lateral and posterior margins are broken but the outline is identifiable (Fig. 3.3). The lateral margin is slightly convex but the middle portion is nearly straight. The scute should be approximately 6 cm in original width, and the axial length is estimated shorter than the width. The axial non-overlap length is 3.6 cm. The dorsal facet of the left anterior wing is partially preserved. The anterior middle portion is incomplete, but the absence of the accessory processes can be deduced. The anterior median incisure is nearly 2 cm in width. The sculptured surface

consists of some elongated oblique sharp ridges that enclose grooves on anterior portion, and predominately transversely extended sharp ridges on posterior portion. This pattern is similar to that of *Synesuchus* (Novikov and Shishkin, 2000) and *Bystrowiella* (Witzmann et al., 2008). Axially, a shallow median groove formed by lateral ridges extends posteriorly for more than half length of the plate.

The posterior median articular plate is damaged for its posterior end and its width is approximately 1/3 the width of the whole plate. The articular plate forms a shelf by the fusion of processes. The dorsal surface of the articular plate is nearly smoothly convex, without distinct 'longitudinal grooves' (Fig. 3.3C). The axial and lateral crests are flat and low. The lateral crests are located slightly ventrally to the axial crest. Lateral to the lateral crest, the area maginalis extends anteriorly below the plate. The area maginalis here seems to correspond to the lateral crest of *Bystrowiella*.

On the ventral surface of the plate, a medial depression (depressio ventralis) is rounded posteriorly to join the ventral process. The posterior margin of the ventral process is not clear but seems posterior to the middle sculpture portion. The smooth oblique crest runs from the lateral margin of the ventral process towards the anterior margin of each wing. Posteriorly, it merges into the free lateral edges of the area maginalis.

Discussion This specimen also can be referred to Bystrowianidae based on the narrow plate bearing broadly separated anterior facets overlapped by preceding plate. It is closely related to *Synesuchus* and *Bystrowiella* than other taxa of Bystrowianidae for the absence of anteromedial articular processes, the presence of smooth oblique crests, the sculpture pattern, and the indistinct crests on the posterior articular plate (Buchwitz et al., 2012; Novikov and Shishkin, 2000; Witzmann et al., 2008). However, it differs from *Synesuchus* and *Bystrowiella* but similar to *Bystrowiana*, *Axitectum*, and *Dromotectum* for the wide posterior articular plate which forms a shelf. Comparing to *Synesuchus* and *Bystrowiella*, the scute is relatively narrower. These characters indicate that *Jiyuanitectum* is more basal than known taxa of Bystrowianidae.

***Dromotectum largum* sp. nov.**

Etymology 'largum', Latin for large.

Holotype IVPP V 4013.1, an incomplete armor scute.

Diagnosis Differentiated from *D. spinosum* by anterior wing more anteriorly extending than accessory process, dorsal facet distinct.

Description The specimen IVPP V 4013.1 (Fig. 3.4), anterior right portion of a plate, is quite large in size. The right lateral margin is slightly convex. The preserved length is 4 cm, and the reconstructed width is approximately 5 cm. The right accessory process is short and wide, more similar to *Dromotectum spinosum* than to *Bystrowiana permira* (Fig. 3.1). The anterior median incisure is relatively wide. The anterior wing is incomplete but still extends more anteriorly than the accessory process. Its dorsal facet is smooth and well developed, and extends far posteriorly. It is thickened in the axial part. The sculpture is formed by rounded

polygonal pits becoming longer at the lateral edge.

On the ventral side, only small part of the ventral process is preserved. Anterior to the ventral process, the ventral depression is rounded and has distinct boundary. Lateral to the ventral process, a narrow and low crest extends anterolaterally and decreases the height anteriorly. It could be the oblique crista.

Discussion This scute is similar to *Bystrowiania* and *Dromotectum* for the presence of accessory process. It is more similar to *Dromotectum spinosum* than to *Bystrowiania* for narrow scute, slightly convex and wide lateral margin, short accessory process, sculpture pattern, and presence of longitudinal crest; so it is referred to *Dromotectum*. It is easily differentiated by *D. spinosum* by the anterior wing more anteriorly extending than the accessory process and with distinct articular surface.

Many small conical teeth (less than 1 cm in height) with distinct ridges are clearly labyrinthodont. Some larger teeth (diameter greater than 1 cm in height) have strongly folded base as in fig. 11 of Young (1979), the teeth are slightly curved with ridges in which two are more prominent and extend to the tip, e.g., HGM 41HIII0447 (Fig. 5.1). These teeth should be fangs of “Labyrinthodontia”. Although we cannot specify the group of these teeth, they could also belong to Chroniosuchia because known materials do not indicate the presence of other “Labyrinthodontia” other than Chroniosuchia. The sculptured bones of “Labyrinthodontia A” (IVPP V 4012) belong to pareiasaur *Honania* (Xu et al., 2014), V 4013.1 is an osterderm palate of Chroniosuchia, and V 4014.2 possibly belongs to a therapsid as showed below.

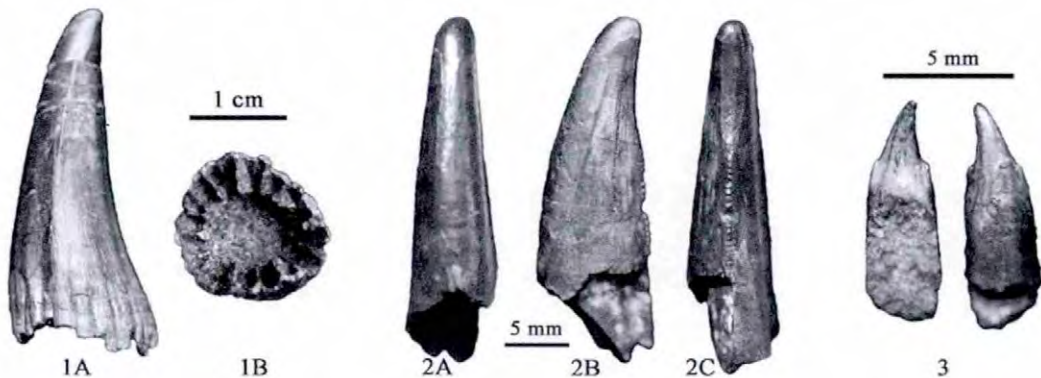


Fig. 5 Teeth of the Jiyuan Fauna

1. a labyrinthodont fang (HGM 41HIII0447) (A) and its cross-section (B); 2. a possible gorgonopsian tooth (HGM 41HIII0448) in anterior (A), lateral (B), and posterior (C) views; 3. holotype of *Hwanghocynodon multienspidus* (IVPP V 4019.1)

Pareiasauria Seeley, 1888

Honania complicidentata Young, 1979

Tsiyuania simplicidentata Young, 1979

Taihangshania imperfacta Young, 1979

Syntypes IVPP V 4015, two complete upper teeth.

Comments Sigogneau-Russell and Sun (1981) pointed out the teeth assigned as holotype of *Taihangshania imperfecta* probably represent worn or digest pareiasaurian teeth. Reexamination of all these teeth confirmed their conclusion. Lee (1997) proposed that the differences between *Tsiyuania* and *Honania* reflect the differences in upper and lower jaw teeth, and declared these two taxa nomina vana. Our recent work shows that most of the bones from this locality, including almost all referred specimens of *Taihangshania imperfecta*, belong to pareiasaur, and these pareiasaur materials represent a valid species. We, therefore, reestablished the name *Honania complicidentata* for this species. We identified two teeth as juvenile pareiasaur teeth: IVPP V 4018.14 (Young 1979: fig. 12g), formerly a gorgonopsian tooth, and V 1049.2, previously a cynodontian tooth (Young 1979: fig. 13b) (Xu et al., 2014). They show the cusp increases in number during ontogeny as in *Deltavjatia* (Kordikova and Khlyupin, 2001).

Therapsida Broom, 1905

? Gorgonopsia Seeley, 1895

Comments In total 17 teeth (IVPP V 4018) were referred to *Wangwusaurus tayuensis*. Young (1979: figs. 10-12) classified them into three groups. Three teeth in fig. 11 (V 4018.6-8) are labyrinthodont fangs, V 4018.14 (fig. 12g) and V 4018.16 (fig. 12i) are pareiasaur teeth, and V 4018.15 (fig. 12h) is not a tooth. Most remaining teeth are fragmentary and they could belong to therapsids, but they do not have enough features to be identified as gorgonopsian teeth. However, an incomplete tooth (HGM 41HIII0448) possibly could be referred to this group (Fig. 5.2). It is 3 cm in height and 1 cm long at the base. It is slightly compressed and curved to some extent and tapers gradually to a point. The tip has a small facet right at its extremity. The anterior margin is smooth, and the dorsal 12 mm is worn from the tip. The posterior serrations are lightly worn for 9 mm from the tip. There are about 20 serrations per 1 cm long. This tooth is similar to the incisor of *Lycosuchus* (van den Heever, 1994), the canine of gorgon *Leontocephalus intactus* (Kemp, 1969) and *Sauroctonus progressus* (Ivakhnenko, 2005). But the distinct wear pattern on this tooth and the shape of the denticles is more similar to the upper canine of *Sauroctonus progressus* and we tentatively identify it as a gorgonopsian canine.

Cynodontia Owen, 1861

***Hwanghocynodon multienspidus* Young, 1979**

Comments Three teeth were referred to this taxon. Among them, two are pareiasaur teeth (Xu et al., 2014). IVPP V 4019.1 (Young, 1979: fig. 13a) is the holotype (Fig. 5.3), with a curved major cusp and two small accessory cusps, and three cingulum cusps lies slightly below and on two sides of the anterior accessory cusp. It is similar to some of the postcanines of *Nanictosaurus* (van Heerden and Rubidge, 1990), *Thrinaxodon* (Crompton, 1963; Abdala et

al., 2013) or *Nanocynodon* (Battail and Surkov, 2000). So we accept the identification of this specimen within Cynodontia and preserve the generic and specific name here.

?Therapsida Broom, 1905

Two vertebrae, IVPP V 4014.2 and HGM 41HIII0446, are referred to therapsids here (Fig. 6). V 4014.2 was referred to *Bystrowiana sinica* by Young (1979). The zygapophyses are closely spaced, especially the postzygapophyses which are less developed than the prezygapophysis. The neural canal is compressed laterally. The transverse process is short and terminates in an elongate diapophysis. The centrum is amphicoelous with anteriorly inclined posterior surface. The distinct facet on the ventral side of the posterior surface indicates the articulation with the intercentrum. On the anterior portion of the ventrolateral surface, the parapophysis is visible that is separated from the posterodorsally located diapophysis by an anterodorsally directed, deep incisure. HGM 41HIII0446 is anteroposteriorly short but slightly higher than V 4014.2. The neural spine is slightly expanded dorsally in V 4014.2 while it shrinks dorsally in HGM 41HIII0446. The dorsal surface is elongated and slightly concaved in V 4014.2, while it is pinched as a pointed tip in HGM 41HIII0446.



Fig. 6 Two possible therapsid vertebrae in anterior (A), lateral (B), and posterior (C) views
1. IVPP V 4014.2; 2. HGM 41HIII0446

Both vertebrae have no paraneural canal, and show no feature of pareiasaur, and they are similar to the caudal of therapsids, such as gorgon *Sauroctonus parringtoni* (Gebauer, 2014), so they are tentatively referred as therapsid caudals: V 4014.2 as anterior caudal, while HGM 41HIII0446 posterior positioned caudal.

3 The correlation of Jiyuan tetrapod fauna

Now, only the following members are identified: *Bystrowiana sinica*, *Jiyuanitectum*

flatum, *Dromotectum largum*, *Honania complicidentata*, *Hwanghocynodon multienspidus*, and a possible gorgonopsian. In Chinese tetrapod assemblages, this one is definitely younger than the Dashankou one and older than the one from the Sunjiagou Formation (*Shansisaurus*, *Shihtienfenia*), but it is hard to correlate to the dicynodonts-dominated assemblages from Xinjiang and Nei Mongol (Daqingshan). More works need to be done to resolve the sequence of Chinese tetrapod assemblages.

In Bystrowianidae, other than *Bystrowiana permira* which came from Vyazniki Assemblage of Permian, all other taxa are Triassic in age (Novikov and Shishkin, 2000; Witzmann et al., 2008). In this fauna, two species are referred to known genera, but *Jiyuanitectum* shows to be more primitive than other known taxa within Bystrowianidae. The phylogenetic position of *Honania* is similar to *Deltavjatia* from the Kotelnich Subassemblage of Sokolki Assemblage (Golubev, 2000). Cynodonts first appeared in Ilinskoe Subassemblage, and *Nanocynodon* comes from Sokolki Subassemblage of Sokolki Assemblage (Golubev, 2000). Gorgonopsian are present in both faunae. Because the pareiasaur assemblage is present in the overlaying Sunjiagou Formation, we roughly correlate this fauna with the slightly younger Ilinskoe Subassemblage of the Sokolki Assemblage. This fauna is roughly correlated with the *Cistecephalus* Assemblage Zone of South Africa, following the former conclusions of Li and Cheng (1995).

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中国上二叠统济源四足动物群——2. 地层、分类学评述及对比

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摘要: 重新研究了济源四足动物群的材料, 表明其以锯齿龙类的复齿河南龙为主体, 还包括至少三种迟滞鳄类和一种犬齿兽, 可能还有一种凶脸兽。根据甲片特征推测, 迟滞鳄类至少包括中国毕氏螈 *Bystrowiana sinica*, 扁平济源盖螈(新属新种) *Jiyuanitectum flatum* gen. et sp. nov. 以及大型脊廊盖螈(新种) *Dromotectum largum* sp. nov.。根据四足动物组合, 济源动物群大致可以与俄罗斯Sokolki组合带的Ilinskoe亚带以及南非的小头兽组合带对比。

关键词: 河南济源, 上二叠统, 上石盒子组, 迟滞鳄类, 锯齿龙类, 凶脸兽类, 犬齿兽类
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